

Thesis /
Reports
Runkel,
K.E. _____

Final Study Plan For A Study Of
PREDATOR - PREY RELATIONSHIPS BETWEEN
CERVIDS AND WOLVES IN THE NORTH FORK OF
THE FLATHEAD RIVER, MONTANA

Nov. 11, 1992

Coop Agreement
University
of
Montana

FINAL REPORT FOR RESEARCH JOINT VENTURE AGMT
No. INT-91617-RJVA with
UNIVERSITY OF MONTANA
FS Contact L. J. Lyon
Co-op Contact: Dr. Dan Pletscher

Final Study plan
for a study of

PREDATOR-PREY RELATIONSHIPS BETWEEN CERVIDS AND WOLVES
IN THE NORTH FORK OF THE FLATHEAD RIVER, MONTANA

by Kyran E. Kunkel
School of Forestry
University of Montana

11 November 1992

INTRODUCTION

Justification and Scope

The U.S. Fish and Wildlife Service (USFWS) is mandated by the Endangered Species Act to produce recovery plans for threatened and endangered species. The gray wolf (Canis lupus) is classified as an endangered species throughout the western United States, including Montana. A plan for wolf recovery in the northern Rocky Mountains was approved in 1987 (USFWS 1987), and part of that plan calls for assessing the effects of wolf recovery on native ungulate populations (Tasks 382, 431, 433). Information is needed on how wolves might affect the population dynamics and behavior of moose (Alces alces), elk (Cervus elaphus), and white-tailed deer (Odocoileus virginianus) in the northern Rockies.

The Montana Department of Fish, Wildlife, and Parks (MDFWP) requires information on the effect wolves may have on ungulate populations so that they can develop alternatives for manipulating habitat or hunting regulations to maintain healthy populations of ungulates.

Glacier and Yellowstone National Parks are core areas for wolf recovery. As part of their mission, national parks provide a unique opportunity to study intact native ecosystems which have been relatively little altered by man (Leopold et al. 1968). Information gathered on wolf recovery in Glacier National Park is

needed by Yellowstone National Park to anticipate effects of wolves in that ecosystem.

Significance

Predator control programs eliminated wolves from their former range in the western U.S. by the 1930's. No documented case of wolf reproduction in the western U.S. occurred until 1986 when a den was found in Glacier National Park (GNP) (Ream et al. 1987). Another den was located in GNP in 1987, and 2 more were documented along the U.S./Canadian border just north and west of GNP (Ream et al. 1991). Approximately 30 wolves (4 packs) currently occupy GNP and the North Fork of the Flathead River (R. Ream, Univ. of Mont., pers. commun.). Ream et al. (1987) have studied food habits and movements of wolves in the North Fork of the Flathead River (NF). Additionally, 3 master's level studies were initiated in 1989 to gather baseline information on mortality and habitat use of white-tailed deer, elk, and moose in the NF. Insights into the relationships between wolves and their prey are just now being elucidated as a result of these studies. Much more research specifically directed at wolf-prey interactions as wolf recovery proceeds will be required before the effects of wolves on their prey can be understood.

Most detailed wolf-prey studies have been conducted where only 1 or 2 main prey species and 1 or 2 top-level carnivores are present and where wolves have been long established (Mech 1966,

Pimlott et al. 1969, Peterson 1977, Fritts and Mech 1981, Nelson and Mech 1981, Peterson et al. 1984, Ballard et al. 1987). White-tailed deer, mule deer (O. hemionus), elk, and moose are all available to NF wolves. Wolves, mountain lions (Felis concolor), black bears (Ursus americanus), and grizzly bears (Ursus arctos) all prey on cervid in the NF. No study has examined in detail the combined effects of wolf and lion predation on cervids nor the effects of these predators on one another. Additionally, the NF area had been without a breeding population of wolves for over 50 years, and cervid populations in the relative security of GNP have probably reached new equilibria with their habitat and other predators. As a result, this area provides a unique opportunity to study the effects of this natural experiment on cervid behavior and populations. Hornocker (1976) stated that violent, destabilizing, predator-prey interactions happen frequently when the interaction is of recent origin. Because the wolf population has been studied in this area from the start of recolonization, baseline information is available for comparisons. Adjacent areas without wolves provide control areas for this study.

Recent developments in landscape ecology theory offer new insights and approaches for examining predator-prey interactions. Prey distribution may be described as a pattern on the landscape. This pattern may influence the process of predation and vice versa. Additionally, patches of suitable habitat may provide refuges from predators and reduce the predation rate (Wolff

1981). Patches of prey and habitat may influence movements, prey selection, and predation rates of wolves which, in turn, affect cervid and wolf population dynamics. Spatial heterogeneity may provide a stabilizing mechanism in predator-prey systems (Tanner 1975). As Turner (1989) states, the effects of pattern on process have not been well studied in any branch of ecology. This type of approach has great potential for predicting effects of wolf recovery on a regional level throughout the northern Rockies.

This proposal is for a 3-year study of the interactions of wolves and cervids in northwestern Montana, with the following objectives.

ESTIMATE THE EFFECTS OF WOLF RECOLONIZATION ON CERVID POPULATION TRENDS.

1. Determine wolf prey selection patterns and cervid vulnerability to predation and the factors affecting these; particularly the effect of spatial relationships between wolves and cervids.
2. Determine how wolves affect seasonal cervid distribution, movements, and habitat use.

OBJECTIVES AND METHODS

Study Area

The study will be conducted in the North Fork of the Flathead River drainage in northwestern Montana and southeastern British Columbia. The study area will encompass the range occupied by wolves in GNP, and extend from Camas Creek in GNP northward to approximately 30 km beyond the Canadian border.

The valley bottom varies from 4-10 km in width and rises from 1,024 m elevation in the south to 1,375 m in the northern part of the study area. Peaks of the Whitefish Range form the western border of the valley, and the Livingstone Range defines the eastern border.

Land east of the North Fork of the Flathead River (south of Canada) lies in GNP. West of the river, land is a mosaic of Flathead National Forest (FNF), Coal Creek State Forest, and private property. The number of year-round human residents within the study area is approximately 40 in Montana and 4 in B.C.

The climate of this area is transitional between a northern Pacific coastal type and a continental type. Mean temperatures range from -9 C in January to 16 C in July (Singer 1979). Snow normally covers the area from mid-November through mid-April. Maximum average snow depth at the Polebridge Ranger Station is 65.4 cm.

Dense lodgepole pine (Pinus contorta) forests dominate most of the North Fork valley, but sub-alpine fir (Abies lasiocarpa),

spruce (*Picea* spp.), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*) communities exist throughout the valley. Abundant meadows and riparian areas are dispersed throughout the study area. Detailed descriptions of vegetative communities in this area have been provided by Habeck (1970), Jenkins (1985), and Krahmer (1989).

Field Procedures and Planned Data Analysis

To estimate the effects of wolf recolonization on cervid population trends.

1. Determine wolf prey selection patterns and cervid vulnerability to predation and the factors affecting these; particularly the effects of spatial relationships between wolves and cervids.

Most wolf-prey studies have focused on the manner in which wolf density, weather, and habitat conditions affect ungulate population dynamics (Mech and Karns 1977, Gasaway et al. 1983, Messier and Crete 1985, Mech et al. 1987, others). Recent research has confirmed earlier findings by Pimlott (1967), Mech (1970), and Keith (1974), who all suggested that predation may, at times, have strong controlling effects on ungulate numbers. As Van Ballenberghe (1987) stated, the question is no longer whether controlling effects occur, but rather under what conditions they occur and how long such conditions last (cf.

Sinclair 1991 and Boutin 1992).

Empirical data from a wide variety of predator-prey systems indicate that spatial relationships, including environmental heterogeneity, significantly affect the ability of predators to encounter and kill prey (Van Ballenberghe 1987). Only recently have spatial relationships between wolves and ungulates been examined as a factor affecting wolf prey selection and ungulate vulnerability (Bergerud et al. 1983, Van Ballenberghe 1987, Bergerud and Snider 1988).

Tanner (1975) modelled many predator/prey systems, including some with 5 species of ungulates, and reported that long search time contributed important elements of stability to predator/prey interactions. Mean densities of moose resulting from predation may vary in different areas due to differences in escape habitat (Bergerud et al. 1983). Populations with widely spaced individuals may support higher ungulate numbers, as do areas with ample escape habitat, due to increased searching time required by wolves and therefore less efficient predation. Bergerud and Snider (1988) proposed a hypothesis that the spacing of predator and prey determines the predation rate and sets equilibrium density, where recruitment equals natural mortality, below that dictated by food. Thus, spatial relationships including prey distribution, predator territory size, and habitat features may have important implications for predator-prey interactions.

Recent developments in landscape ecology and spatial analysis theory along with the development of Geographic

Information Systems have made researchers aware of the importance of spatial relationships and provided them with tools for quantitatively analyzing these relationships.

The distribution and abundance of cervids in wolf territories will be measured and related to predator avoidance and escape strategies used by cervids, and to foraging and prey selection strategies employed by wolves. Such an analysis should provide valuable information about factors affecting cervid vulnerability to predation and how this in turn affects wolf predation and cervid population dynamics.

Spatial relationships between cervids and wolves will be analyzed with an appropriate GIS. Overlay techniques will be used to display unions and intersections of cervid distribution, wolf locations, vegetative cover, physical characteristics (escape terrain) and snow cover (when applicable) and to discover conditions or factors affecting cervid vulnerability to predation and wolf prey selection. Distribution of cervids in relation to predation vulnerability and to wolf prey selection will be described using landscape ecology techniques to examine the effect of pattern (prey distribution) on the predation process. The effects of wolf recolonization (disturbance factor) on prey heterogeneity will also be examined. Patches of prey will be defined in terms of relative prey density, biomass, and diversity. Size, shape, accessibility, and configuration of patches will also be measured. Linkages between patches will be described (Pielou 1977, Forman and Godron 1986). Proximity

analysis, neighborhood analysis (Tomlin 1983, Berry 1987, Burrough 1987), and distance-based tests of independence (Diggle and Cox 1983) will be used to quantify spatial relationships between wolves and cervids. These will be related to prey vulnerability and prey selection by wolves. Such an examination will indicate what the important cues are that wolves use to select hunting sites (i.e., prey density, cover type and density, topography).

2. Determine how wolves affect seasonal cervid distribution, movements, and habitat use.

Most wolf-prey studies have focused on the effects of wolves on the population dynamics of their prey (Mech and Karns 1977, Gasaway et al. 1983, Messier and Crete 1985, Peterson et al. 1984, Bergerud and Elliot 1986, Ballard et al. 1987, others). Only recently have these studies begun to examine the effects of wolves on ungulate movements, distribution, and habitat selection.

Miller (1975) reported that wolf-killed caribou (Rangifer tarandus) were not randomly distributed and that certain sites must provide wolves with an advantage over their prey. Peterson and Woolington (1981) found most wolf-killed moose on the Kenai Peninsula in old burns, often associated with small stands of timber remaining in the burn. Stephens and Peterson (1984) concluded that moose seek conifer cover and its associated structure to reduce attack rates by wolves.

Bergerud and Page (1987) provided evidence that caribou space themselves out and disperse into the mountains to reduce risk of predation. Caribou and moose often use shorelines to avoid and escape wolves (Stephens and Peterson 1984, Bergerud 1985, Ferguson et al. 1988). Bergerud et al. (1984) indicated that caribou seek high mountain slopes as an antipredator tactic.

Mech (1977) found that wolf predation affects the distribution of deer within wolf territories. In northeastern Minnesota, deer density was greater on wolf territory edges than in interior regions due to reduced predation pressure along these edges. Distribution of ungulates in wolf territories may also affect the wolves' search rate for prey and affect the rate of predation (Bergerud et al 1983).

Hatter (1982) found that wolves contributed to increased summer range movements of elk cow-calf groups and caused black-tailed deer to bypass spring ranges where wolf predation was intense. Moose cow-calf movements and home ranges were larger when wolves and brown bears were present than in their absence (Ballard et al. 1980). Predators are also hypothesized to keep ungulates moving on their winter ranges (Leopold 1933, Hunter and Yeager 1956, Hornocker 1970).

Sweeney et al. (1971) reported that radio-collared deer moved away from the disturbance of hounds chasing other deer, sometimes into areas that offered more protection (dense cover or swamps). Dasmann and Taber (1956:155) concluded that, within its home range, each deer usually had a preferred area for escape and

would head for that area even if other cover was close by.

Almost nothing is known about wolf avoidance strategies of elk. Janz (cited in Hatter 1982) believed that increases in elk group size and shifts in distribution have occurred coincident with increasing wolf populations. Hatter (1982) hypothesized that elk may decrease their use of open habitats as wolf densities increase. Additionally, elk may increase their use of higher elevations as wolf predation intensifies. Hornocker (1970) observed that elk avoided areas where a mountain lion had made a kill, often crossing to the far end of the watershed and in some instances leaving to enter a different drainage. Deer reduce their vulnerability to wolves and coyotes during winter by concentrating in yards (Nelson and Mech 1981, Messier and Barrette 1985) and as a result may be less susceptible to predation than elk, who don't employ such a strategy. Clearly, research is needed to test these hypotheses and estimate elk vulnerability to predation and how wolves will affect elk behavior and populations.

The wolf population recolonizing the NF provides an excellent opportunity to study how wolves may cause changes in distribution, movements, and habitat use by cervids who have been without wolf predation pressure for more than 50 years. Cervids may use habitat (or behave) differently when wolves are near, or cervids that survive the presence of wolves may use habitat differently than those that do not survive.

Additionally, wolves in the NF have a very linear home

range, moving up and down the river throughout the year. Except during the denning season, wolves tend to stay in an area for only a few days, then move to another area for several days to a week, and so forth (Ream et al. 1987). This situation makes it possible to study the effect of wolves on cervid habitat use, movements, and distribution by comparing cervid locations when wolves are nearby (wolves present) with cervid locations when wolves are in another area (wolves absent).

To determine wolf prey selection patterns and cervid vulnerability to predation and the factors affecting these.

1. Evaluate the combined influence of lion, bear, and wolf predation on cervid population trends.

One of the primary concerns about wolf recovery for the public and for wildlife management agencies in the western U.S. is what effect wolf predation will have on ungulate populations. Predation by wolves on ungulates continues to be a source of public controversy and scientific debate (cf. Van Ballenberghe 1985, 1989; Bergerud and Ballard 1988, 1989). Most recent studies indicate that under certain conditions, wolf predation may significantly limit the growth of some ungulate populations (Gasaway et al. 1983, Bergerud and Elliot 1986, Bergerud and Snider 1988) especially in areas where other predators are also found. Other researchers have found that wolves have little

effect on ungulate population growth and that other factors are more important (Thompson and Peterson 1988, Fuller 1990). Undoubtedly both cases can be true, and the particular area and the specific ungulate and wolf populations are critical in determining the effect. Little information, however, is available on the effects of wolves on the diverse prey populations in the northern Rockies, especially elk (Carbyn 1974, Weaver 1979, Gunson 1986). Hebert et al. (1981) suggested that predation pressure on deer is more severe in wolf territories with elk concentrations probably because elk provide a source of alternate prey enabling wolves to continue exerting intense pressure on deer.

2. Evaluate foraging and prey selection strategies of wolves and the degree of niche overlap between wolves and lions.

Mountain lions in Montana are increasing their range and numbers and their effect on ungulate populations may be more significant than previously believed (S. Riley, Mont. Dep. of Fish, Wildl., and Parks, pers. commun.). Almost no information is known on wolf/lion predation niche overlap and the combined effects of that predation on ungulates. This type of information is critical for wildlife and land management agencies to enable them to anticipate these effects and develop management options.

During winter, greater overlap in habitat use and prey

selection may be expected because prey are congregated in the valley bottom. The killing of lions by wolves has been recorded on 2 occasions in our study area. How resources are partitioned and how wolf/lion communities are structured is unknown as are the factors influencing these parameters. What effect this, in turn, has on prey selection and on the prey community is unknown. Changes in habitat use, behavior, and distribution brought about by wolves may affect vulnerability to mountain lions.

Interference competition and environmental factors may influence habitat selection, space use, and prey selection in wolves and lions. The effect this may have on cervid population dynamics and behavior as well as the structure of the carnivore community needs to be explored.

A study of lion ecology in the NF is being initiated this winter by the Wildlife Research Institute (WRI). Working in conjunction with this study will provide an excellent opportunity to examine wolf/lion relationships and the effects of these predators on the prey population in the NF.

3. Evaluate the effects of snow conditions on cervid vulnerability to predation.

Deep snow may restrict options for habitat selection by cervids (Jenkins and Wright 1988). Snow depth and characteristics may affect the distributions and spatial overlap of moose, elk, and white-tailed deer. Snow conditions may also

predispose prey to wolf predation. Gross indications of the importance of snow conditions on predation have long been known (Mech and Frenzel 1971, Mech and Karns 1977, Peterson 1977), but the precise role of snow conditions in increasing vulnerability of prey is just beginning to be defined (Nelson and Mech 1986, Mech et al. 1987). Snow depth and conditions affect ungulate mobility and ungulate nutritional condition, which in turn affect vulnerability to predation. One cervid species may be more vulnerable than others to predation in differing snow conditions (Boyd et al. submitted). By collecting and analyzing snow-urine samples from elk, DelGuidice et al. (1991) recently reported a correlation of poorer ungulate condition with increasing snow depth in Yellowstone National Park.

A wildfire in 1988 burned a total of 14,096 ha in the NF. Complete removal of forest canopy occurred in several areas known to provide forage and/or shelter for white-tailed deer, elk, and moose. This structural change affects snow depth and characteristics and may affect forage available to cervids.

To evaluate the combined influence of lion, wolf, and bear predation on cervid population trends.

1. Estimate cause-specific mortality rates of adult female elk, moose, and white-tailed deer.
2. Estimate yearly elk populations, production, and calf survival in the NF.
3. Estimate yearly moose populations and calf survival.

4. Estimate yearly white-tailed deer population trends and fawn survival.
5. Estimate wolf numbers and production yearly by observation during aerial tracking.
6. Estimate wolf predation rates by backtracking wolves.

To estimate cause-specific mortality rates of adult female elk, moose, and white-tailed deer.

1. Capture, age (Gilbert 1966), and place mortality-sensing radio collars on 30 adult female white-tailed deer, elk, and moose.
2. Monitor radiocollared animals for mortality.
3. Determine cause of death when mortality occurs.
4. Analyze mortality data with methods described by Heisey and Fuller (1985) and computer software MICROMORT (version 1.3, Heisey 1987). Rates will be compared among seasons and between years by Z tests based on radio-days of survival. Age-specific mortality rates will be compared if sample size allows. Survival rates from this study will be compared to the rates from the study being conducted by Montana Department of Fish, Wildlife, and Parks (MDFWP) west of the Whitefish divide where wolf density is significantly less.

To capture and radio-collar 30 adult female white-tailed deer, elk, and moose.

1. Place clover traps baited with alfalfa hay in southern,

central, and northern portions of deer and elk winter ranges (Rachael 1992).

2. Dart moose from a helicopter on their winter range.

To determine cause of death when mortality occurs.

1. Examine kill sites and carcasses for predator involvement.
2. Necropsy carcasses to determine cause of death (O'Gara 1978).

To estimate yearly elk populations, production, and calf survival.

1. Estimate calf production by visually locating cows in the spring.
2. Classify elk by sex and age from helicopter.
3. Conduct winter counts of elk by helicopter.
4. Compare spring cow/calf ratios to winter ratios to estimate calf survival.
5. Monitor a hunter big game check station to estimate age and sex composition of the elk population and estimate hunter effort and success which has been found to be significantly correlated with population size (Freddy 1982, Roseberry and Wolff 1991). Similar data gathered by MDFWP at other check stations in areas without wolves and will be compared to the NF.

To conduct winter counts of elk by helicopter.

1. Stratify the study area into classes based on elk density.
2. Search the study area by helicopter following the procedures of Unsworth et al. (1991).
3. Adjust population estimates to account for unseen elk with a computer program (Aerial Survey; Unsworth et al. 1991) that provides a sightability model for elk (Samuel et al. 1987) which will be used to estimate elk abundance and distribution based on the aerial survey.

To estimate the yearly moose population and calf survival.

1. Conduct aerial surveys for moose in early winter using a stratified, random design based on relative moose densities (Gasaway et al. 1986). Transects at 0.4-0.8 km intervals will be flown and areas where moose are seen will be circled to count additional moose.
2. Use sightability correction factors based on sightability of radiocollared moose.

To estimate yearly white-tailed deer population trends and fawn survival.

1. Conduct deer pellet-group counts (Tucker 1991) along 80 uncleared 1.8 m-radius plots on each of 11 pairs of transects during spring. Transects will be distributed to encompass the entire range of habitat types and geographic

variation in the area. The sample size of plots will be sufficient to detect a 20% change in the index with 90% certainty. The Kruskal-Wallis test will be used to test for differences in variances among transects, and the Mann-Whitney U test will be used to compare results among years. Results will also be compared to counts made by MDFWP on the west side of the Whitefish divide where wolf density is significantly lower than the NF.

2. Conduct roadside counts of deer in open fields in the spring to estimate doe/fawn ratios and classify deer by sex and compare to the west side of Whitefish divide.
3. Compare spring doe/fawn ratios to doe fetal rates to estimate fawn survival.
4. Monitor a hunter big game check station to estimate age and sex composition of the deer population and estimate hunter effort and success to compare to other check stations in areas without wolves.

To estimate wolf numbers and production yearly by observation during aerial tracking.

1. Capture wolves in leghold traps and fit with radiocollars.
2. Locate wolves by use of aerial telemetry.

To estimate wolf predation rates by backtracking.

1. Locate radiocollared wolves on the ground and follow

their tracks to locate kills.

2. Track wolves daily and locate all kills made over a given interval to estimate predation rate.

To evaluate foraging and prey selection strategies of wolves and the degree of niche overlap between wolves and lions.

1. Determine wolf food habits and compare to lion food habits.
2. Determine wolf space and habitat use and compare to lion space and habitat use and prey availability.
3. Compare wolf kill locations to lion kill locations and locations of surviving cervids.

To determine wolf food habits and compare to lion food habits.

1. Locate wolf kills by backtracking wolves and determine species of kill.
2. Estimate frequency of occurrence, relative biomass, and relative numbers of prey of each species consumed by wolves by analyzing scats (Floyd et al. 1978).
3. Estimate wolf-caused mortality rates in radiocollared cervids and compare to lion-caused mortality rates.
4. Compare wolf food habit data to data obtained by WRI lion project.

To estimate wolf-caused mortality rates in radiocollared cervids and compare to lion-caused mortality rates.

1. Determine predator responsible in deaths of radiocollared cervids.
2. Compare wolf-caused and lion-caused mortality rates with MICROMORT computer program.

To determine wolf space and habitat use and compare to lion space and habitat use and prey availability.

1. Locate wolves by radiotelemetry and plot locations on topographic maps.
2. Locate wolf travel routes by backtracking.
3. Compare percent distances of wolf tracks in the snow (from backtracking) to the percentage of that habitat within the wolf's territory.
4. Depict use of space by radio-collared wolves (home range) in 3 dimensions as a utilization distribution (UD) in which time (or frequency of locations) is plotted on the z-axis to account for differential use of portions the animal's home range (Van Winkle 1975). Compare utilization distribution patterns of different wolf packs and relate to prey availability.
5. Use multiresponse permutation procedures (MRPP), a nonparametric statistical test (Mielke et al. 1976), to detect significant shifts in use patterns of home range among wolf packs (Saltz and Alkon 1989). This test is similar in purpose to the t test or the one-way analysis of variance F test, but it does not depend on the assumptions

that the data are distributed normally or that variances between groups are equal (Zimmerman et al. 1985). The P values associated with each pair of comparisons of wolf occurrence (presence vs absence) indicate the probability that the distribution of the cervid locations were the same between occurrences.

6. Measure the number of tracks of prey species intercepted by wolf tracks for an index of the different prey species available to wolves. Ski 2 100m long perpendicular (to wolf travel routes) transects randomly located along each day's wolf travel route to count cervid tracks for incorporation into this index.

7. Use lion track interceptions of wolf tracks as an estimate of wolf/lion space overlap.

8. Use chi-square analysis to test for differential use of habitat features between wolves and lions by using data obtained from the WRI lion project.

To compare wolf kill locations to lion kill locations and locations of surviving cervids.

1. Locate wolf kills by backtracking.
2. Monitor radiocollared cervids and examine mortality sites.
3. Obtain additional lion kill location data from the WRI lion project.
4. Locate surviving cervids by telemetry.

5. Measure habitat and spatial variables at killsites and cervid relocations.
6. Subject the habitat data set to Factor Analysis (Morrison 1976) to reduce its dimensionality. Discriminant Function Analysis (DFA) of factor scores will be used to identify variables (factors) which distinguish species habitat use from habitat availability. Habitat availability will be estimated by a randomly selected sample of points which lie within the seasonal distribution of each species. Habitat selection will be inferred from the separation between habitat use and habitat availability matrices (Edge et al. 1987). Multivariate analysis of variance (MANOVA; Morrison 1976) will be used to compare habitats used by cervids killed by wolves to those of surviving animals or animals killed by other predators to estimate factors that may cause cervids to be more vulnerable to a particular predator.

To measure habitat and spatial variables at killsites and cervid relocations.

1. Measure snow depth at killsites and relocations.
2. Estimate cervid distribution (and availability) around killsites and relocations.
3. Measure vegetation features at and surrounding killsites and relocations.
4. Measure slope, aspect, elevation, distance to water and

roads at killsites and relocations using a GIS.

5. Determine spatial location of kills in wolf and lion territories by overlaying killsites on territories to determine if kills occur more in core or edge areas of territories.

To estimate cervid distribution around killsites and relocations.

1. Conduct cervid track transects throughout the NF.
2. Ski 2 perpendicular cervid track transects 100 m long centered on the killsite or relocation.

To conduct cervid track transects throughout the NF.

1. Ski 20 3.2-4.8 km long parallel transects 1.6 km apart located between Camas Creek and the Canadian border. Transects will be divided into segments based on vegetation type and surveyed every 7-30 days depending on snow conditions.
2. Count number of times cervid tracks intercept the transects and indicate the species.

To measure vegetative features at and surrounding killsites and relocations.

1. Digitize locations into a GIS.
2. Maps, aerial photos, and remotely sensed data that have been digitized into a GIS will be used to determine slope,

aspect, elevation, cover type, amount of habitat edge, mean size of habitat, forage type and spatial diversity (Pielou 1975) at telemetry locations. Distance from telemetry locations to the nearest road, the nearest water, and the nearest human habitation will be measured.

To evaluate the effects of snow conditions on cervid vulnerability.

1. Determine the effects of snow conditions on cervid distribution.
2. Determine the effects of snow conditions on cervid condition by collecting snow-urine samples and examining wolf kills.
3. Compare wolf-caused mortality rates among years of differing snow depths using MICROMORT and regression techniques.

To determine the effects of snow conditions on cervid distribution.

1. Estimate cervid distribution by track surveys using the same transects used to estimate cervid distribution around killsites and relocations.
2. Measure snow depth along the track transects.
3. Estimate preferential use of snow depths by cervids using use versus availability methods (Neu et al. 1974).
4. Use distance-based tests of independence (Diggle and Cox

1983) to measure association between wolves and cervids to determine if cervids and wolves are located in an independent fashion or if cervids exhibit repulsion under varying conditions.

To determine the effects of snow conditions on cervid condition.

1. Collect 30 snow-urine samples monthly from elk and deer from a northern, central, and southern collection areas along the track transects (used to determine cervid distribution) during 3 sampling periods (DelGiudice et al. 1991).
2. Chemically analyze samples to determine sodium:creatinine and potassium:creatinine ratios and compare these to values obtained from deer and elk of known condition (DelGiudice et al. 1991).
3. Use ANOVA and the least squares means test to compare sampling areas and periods.

To determine how wolves affect seasonal cervid distribution, movements, and habitat use.

1. Determine avoidance and escape strategies used by cervids.
2. Determine cervid distribution in relation to wolf pack and lion territories by estimating cervid distribution from track survey transects and aerial surveys (the same surveys

used to determine cervid distribution) and comparing this to an expected random distribution by drawing concentric zones around geographic centers of wolf territories. Wolf use of these zones will also be quantified.

3. Determine cervid distribution in relation to habitat features and compare to data from areas with no wolves.

To determine avoidance and escape strategies used by cervids.

1. Determine movements, distribution and cervid utilization of habitat features in relation to location of wolves and lions.
2. Determine elk group size in presence versus absence of wolves.
3. Compare elk calving site habitat characteristics to wolf den site habitat characteristics.

To determine cervid movements, distribution, and utilization of habitat features in relation to location of wolves and lions.

1. Depict use of space by radio-collared cervids (home range) in 3 dimensions as a utilization distribution (UD) in which time (or frequency of locations) is plotted on the z-axis to account for differential use of portions the animal's home range (Van Winkle 1975). Home ranges will also be delineated and mapped by conventional methods (Computer Software Homerange, Univ. of Idaho).
2. Compare home ranges of cervids from relocations when

wolves are present versus when wolves are absent (Saltz and Alkon 1989).

3. Use Ivlev's index of habitat selection (Ivlev 1961) to compare core areas of home ranges of cervids when wolves are present to when wolves are absent.

4. Measure slope, aspect, elevation, cover type, edge, habitat size, spatial diversity, and distance to roads and water at telemetry locations of cervids when wolves are present and when absent and compare with discriminant function analysis. Subject the habitat data set to Factor Analysis (Morrison 1976) to reduce its dimensionality. Discriminant Function Analysis (DFA) of factor scores will be used to identify variables (factors) which distinguish species habitat use from habitat availability. Habitat availability will be estimated by a randomly selected sample of points which lie within the seasonal distribution of each species. Habitat selection will be inferred from the separation between habitat use and habitat availability matrices (Edge et al. 1987). The identified variables (factors) will be used to discriminate among habitat use by the 3 species. Multivariate analysis of variance (MANOVA; Morrison 1976) will be used to assess the effect of wolf predation on seasonal habitat selection by determining whether the mean vectors of habitat factor scores for the three species differ in the presence and absence of wolves.
5. Use multiresponse permutation procedures (MRPP), a

nonparametric statistical test (Mielke et al. 1976), to compare distributions of winter cervid locations when wolves are present versus when wolves are absent to detect significant shifts in location or use patterns of home ranges. This test is similar in purpose to the t test or the one-way analysis of variance F test, but it does not depend on the assumptions that the data are distributed normally or that variances between groups are equal (Zimmerman et al. 1985). The P values associated with each pair of comparisons of wolf occurrence (presence vs absence) indicate the probability that the distribution of the cervid locations were the same between occurrences.

6. Use distance-based tests of independence (Diggle and Cox 1983) to measure association between wolves and cervids to determine if cervids and wolves are located in an independent fashion or if cervids exhibit repulsion.

7. Use Horn's (1966) index of overlap to compare cover type and space parameters between wolves and each cervid species.

8. Relate these associations and patterns to prey availability, prey selection, and predation rates of wolves.

To determine cervid distribution in relation to habitat features and compare to data from areas with no wolves.

1. Determine cervid distribution through telemetry at weekly intervals.
2. Determine slope, aspect, elevation, cover type, edge,

habitat size, spatial diversity, and distance to roads and water at each location with maps, aerial photos, and a GIS.

LITERATURE CITED

- Ballard, W. B., C. L. Gardner, and S. D. Miller. 1980. Influence of predators on summer movements of moose in southcentral Alaska. *Alces* 16:338-359.
- _____, J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildl. Monogr.* 98. 54pp.
- Bergerud, A. T. 1985. Antipredator strategies of caribou: dispersion along shorelines. *Can. J. Zool.* 63:1324-1329.
- _____, and W. B. Ballard. 1988. Wolf predation on caribou: the Nelchina case history, a different interpretation. *J. Wildl. Manage.* 52:344-357.
- _____, and _____. 1989. Wolf predation on the Nelchina caribou herd: a reply. *J. Wildl. Manage.* 53:251-259.
- _____, H. E. Butler, D. R. Miller. 1984. Antipredator tactics of calving caribou: dispersion in mountains. *Can. J. Zool.* 62:1566-1575.
- _____, and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. *Can. J. Zool.* 64:1515-1529.
- _____, and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. *Can. J. Zool.* 65:1597-1606.
- _____, and B. Snider. 1988. Predation in the dynamics of moose populations: a reply. *J. Wildl. Manage.* 52:559-564.
- _____, W. Wyett, and B. Snider. 1983. The role of wolf predation in limiting a moose population. *J. Wildl. Manage.* 47:977-988.
- Berry, J. K. 1987. Computer-assisted map analysis: potential and pitfalls. *Photogrammetric Engineering and Remote Sensing* 53:1405-1410.
- Boutin, S. 1992. Predation and moose population dynamics: a critique. *J. Wildl. Manage.* 56:116-127.
- Boyd, D., R. Ream and M. Fairchild. submitted 1992. Characteristics of prey killed by wolves in the Glacier National Park area.
- Burrough, P. A. 1987. Principles of Geographic Information Systems for land resource assessment. Monograph on Soil and Resources Survey No. 12. Clarendon Press, Oxford. 194 pp.

- Carbyn, L. N. 1974. Wolf predation and behavioral interactions with elk and other ungulates in an area of high prey diversity. Ph.D. Thesis. Univ. Toronto, Toronto. 233 pp.
- Dasmann, R. F. and R. D. Taber. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. *J. Mammal.* 37:143-164.
- DelGiudice, G. D., F. J. Singer, and U. S. Seal. 1991. Physiological assessment of winter nutritional deprivation in elk of Yellowstone National Park. *J. Wildl. Manage.* 55:653-664.
- Diggle, P. J. and T. F. Cox. 1983. Some distance-based tests of independence for sparsely-sampled multivariate spatial point patterns. *Int. Stat. Rev.* 51:11-23.
- Edge, W. D., C. L. Marcum, and S. L. Olson-Edge. 1987. Summer habitat selection by elk in western Montana: a multivariate approach. *J. Wildl. Manage.* 51:844-851.
- Ferguson, S. H., A. T. Bergerud, and R. Ferguson. 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. *Oecologia* 76:236-245.
- Floyd, T. J., L. D. Mech, and P. A. Jordan. 1978. Relating wolf scat content to prey consumed. *J. Wildl. Manage.* 42:528-532.
- Forman, R. T. T. and M. Godron. 1986. Landscape ecology. John Wiley and Sons, New York, N.Y. 619 pp.
- Freddy, D. J. 1982. Predicting mule deer harvest in Middle Park, Colorado. *J. Wildl. Manage.* 46:801-806.
- Fritts, S. H., and L. D. Mech. 1981. Dynamics, movements, and feeding ecology of a newly-protected wolf population in northwestern Minnesota. *Wildl. Monogr.* 80. 79 pp.
- . 1990. Dynamics of a declining white-tailed deer population in north-central Minnesota. *Wildl. Monogr.* 110. 37 pp.
- Gasaway, W. C., S. D. Dubois, D. J. Reed, and S. J. Harbo. 1986. Estimating moose population parameters from aerial surveys. *Biol. Pap. Univ. Alaska*, No. 22. Fairbanks. 108 pp.
- , R. O. Stephenson, J. L. Davies, P. K. Shepard, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. *Wildl. Monogr.* 84. 50 pp.

- Gilbert, F. F. 1966. Aging white-tailed deer by annuli in the cementum of the first incisor. *J. Wildl. Manage.* 30:200-202.
- Gunson, J. R. 1986. Wolves and elk in Alberta's Brazeau country. *Bugle*. Winter 1986/87:29-33.
- Habeck, J. R. 1970. The vegetation of Glacier National Park. Natl. Park Serv. and Univ. Montana, Missoula. 123 pp.
- Hatter, I. W. 1982. Predator-ungulate relationships in second growth forests on Vancouver Island. Problem Analysis, IWIFR-5, Ministry of Environment and Forests. Victoria, B. C. 54 pp.
- Hebert, D. M., J. Youds, R. Davies, H. Langin, D. Janz, and G. W. Smith. 1981. Preliminary investigations of the Vancouver Island wolf prey relationships. *Int. Wolf Symp.*, Portland, Oreg.
- Heisey, D. M. 1987. MICROMORT user's guide. NH analytical hardware, St. Paul, Minn. 10 pp.
- _____ and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *J. Wildl. Manage.* 49:668-674.
- Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. *Am. Nat.* 100:419-424.
- Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildl. Monogr.* 21. 39 pp.
- _____. 1976. The possible influence of the mountain lion on mule deer populations. Pages 107-109 in G. Workman and T. Blow eds. *Mule deer decline in the West*, a Symposium. Utah State Univ. 134 pp.
- Hunter, G. N. and L. E. Yeager. 1956. Management of the mule deer. Pages 449-482 in *The Deer of North America*. W. P. Taylor, ed. The Stackpole Co., Harrisburg, Penn. 668 pp.
- Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Conn. 302 pp.
- Jenkins, K. J. 1985. Winter habitat and niche relationships of sympatric cervids along the North Fork of the Flathead River, Montana. Ph.D. Thesis, Univ. of Idaho, Moscow. 183 pp.

- Jenkins, K. J. and R. G. Wright. 1988. Resource partitioning and competition among cervids in the northern Rocky Mountains. *J. Appl. Ecol.* 25:11-24.
- Keith, L. B. 1974. Some features of population dynamics in mammals. *Trans. Int. Congr. Game Biol.* 11:17-58.
- Krahmer, R. W. 1989. Seasonal habitat relationships of white-tailed deer in northwestern Montana. M.S. Thesis, Univ. of Montana, Missoula. 104 pp.
- Leopold, A. 1933. *Game Management*. Charles Scribner's Sons. New York. 481 pp.
- Leopold, A. S., S. A. Cain, C. M. Cottam, and T. L. Kimball. 1963. Wildlife management in the national parks. *Trans. N. Am. Nat. Res. Conf.* 28:28-45.
- Mech, L. D. 1966. The wolves of Isle Royale. U. S. Natl. Park Serv. Fauna Ser. 7. U. S. Govt. Printing Off. Washington D. C. 210 pp.
- _____. 1970. The wolf: the ecology and behavior of an endangered species. *Nat Hist. Press*, Garden City, NY. 384 pp.
- _____. 1974. Current techniques in the study of elusive wilderness carnivores. *Proc. Int. Congr. Game Biol.* 11:315-322.
- _____. 1977. Wolf-pack buffer zones as prey reservoirs. *Science*. 198:320-321.
- _____. and L. D. Frenzel. 1971. Ecological studies of the timber wolf in northeastern Minnesota. *For. Serv. Paper NC-52*, North Cent. For. Exp. Stn., St. Paul, MN. 62 pp.
- _____. and P. D. Karns. 1977. Role of the wolf in a deer decline in the Superior National Forest. *USDA For. Serv. Res. Paper. NC-141*. 23 pp.
- _____. R. E. McRoberts, R. O. Peterson, and R. E. Page. 1987. Relationship of deer and moose populations to previous winters' snow. *J. Animal Ecol.* 56:615-627.
- Messier, F. and C. Barrette. 1985. The efficiency of yarding behaviour by white-tailed deer as an antipredator strategy. *Can. J. Zool.* 63:785-789.
- _____. and M. Crete. 1985. Moose-wolf dynamics and the natural regulation of moose populations. *Oecologia* 65:503-512.

- Mielke, P. W., K. J. Berry, and E. S. Johnson. 1976. Multiresponse permutation procedures for a priori classifications. *Communications in Statistics-Theory and Methods* A5:1427-1437.
- Miller, D. R. 1975. Observation of wolf predation on barren ground caribou in winter. Pages 209-220 in J. R. Luick, P. C. Lent, D. R. Klein, and R. B. White, eds. *Proc. 1st Int. Reindeer/Caribou Symp. Occ. Pap. No. 2, Inst. Arctic Biology, Univ. of Alaska College*. 551 pp.
- Morrison, D. F. 1976. *Multivariate statistical methods*. 2nd ed. McGraw-Hill, New York, N.Y. 415 pp.
- Nelson, M. E., and L. D. Mech. 1981. Deer social organization and wolf predation in northeastern Minnesota. *Wildl. Monogr.* 77. 53 pp.
- _____, and _____. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. *J. Wildl. Manage.* 50:471-474.
- Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38:541-545.
- O'Gara. 1978. Differential characteristics of predator kills. Pages 380-393 in *Proc. 8th Biennial Pronghorn Antelope Workshop, Jasper, Alberta*.
- Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. *U. S. Natl. Park Serv. Sci. Monogr. Ser.* 11. 210 pp.
- _____, and J. D. Woolington. 1981. *Wolves of the Kenai Peninsula, Alaska*. Unpubl. Report. 117 pp.
- _____, and T. N. Bailey. 1984. *Wolves of the Kenai Peninsula, Alaska*. *Wildl. Monogr.* 88. 52 pp.
- Pielou, E. C. 1975. *Ecological diversity*. John Wiley and Sons, New York, N.Y. 165 pp.
- _____. 1977. *Mathematical ecology*. John Wiley and Sons, New York, N.Y. 385 pp.
- Pimlott, D. H. 1967. Wolf predation and ungulate populations. *Am. Zool.* 7:267-278.
- _____, J. A. Shannon, and G. B. Kolenosky. 1969. The ecology of the timber wolf in Algonquin Provincial Park. *Ontario Dep. Lands and For. Restoration Rep. No. 87*. 92 pp.

- Rachael, J. S. 1992. Mortality and seasonal distribution of white-tailed deer in an area recently recolonized by wolves. M. S. Thesis, Univ of Montana, Missoula. 115 pp.
- Ream, R. R., M. W. Fairchild, D. A. Boyd, and D. H. Pletscher. 1987. Wolf monitoring and research in and adjacent to Glacier National Park. Unpublished report, Univ. Montana, Missoula. 41 pp.
- _____, _____, and _____. 1991. Population dynamics and home range changes in a colonizing wolf population. Pages 349-366 in R. B. Keiter and M. S. Boyce, eds., The greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale Univ. Press, New Haven.
- Roseberry, J. L. and A. Woolf. 1991. A comparative evaluation of techniques for analyzing white-tailed deer harvest data. Wildl. Monogr 117. 59 pp.
- Saltz, D. and P. U. Alkon. 1989. On the spatial behavior of Indian crested porcupines. J. Zool. 217:255-266.
- Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. J. Wildl. Manage. 51:622-630.
- Sinclair, A. R. E. 1991. Science and the practice of wildlife management. J. Wildl. Manage. 55:767-773.
- Singer, F. J. 1979. Habitat partitioning and wildfire relationships of cervids in Glacier National Park, Montana. J. Wildl. Manage. 43:437-444.
- _____, and E. O. Garton. 1988. Visibility of northern Yellowstone elk from fixed-wing aircraft and helicopter. Pages 1-21 in F. J. Singer, ed. Elk ecology studies. 1987 annual report. Yellowstone Natl. Park, WY.
- Stephens, P. W. and R. O. Peterson. 1984. Wolf-avoidance strategies of moose. Holarc. Ecol. 7:239-244.
- Sweeney, J. R., R. L. Marchinton, and J. M. Sweeney. 1971. Responses of radio-monitored white-tailed deer chased by hunting dogs. J. Wildl. Manage. 35:707-716.
- Tanner, J. T. 1975. The stability and intrinsic growth rates of prey and predator populations. Ecology 56:855-867.
- Thompson, I. D. and R. O. Peterson. 1988. Does wolf predation limit the moose population in Pukaskwa Park?: a comment. J. Wildl. Manage. 52:556-559.

- Tomlin, C. D. 1983. Digital cartographic modelling techniques in environmental management. Ph.D. Thesis. Yale Univ., New Haven.
- Tucker, P. A. 1991. Evaluation of techniques to monitor white-tailed deer in the North Fork of the Flathead River, Montana. M.S. Thesis, Univ. of Montana, Missoula. 90 pp.
- Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annu. Rev. Ecol. Syst.* 20:171-197.
- U.S. Fish and Wildlife Service. 1987. Northern Rocky Mountain wolf recovery plan. U.S. Fish and Wildlife Service, Denver, Colorado. 119 pp.
- Unsworth, J. W., F. A. Leban, G. A. Sargeant, E. O. Garton, M. A. Hurley, and J. P. Pope. 1991. Aerial survey: user's manual. Idaho Dep. Fish and Game, Boise, ID. 54 pp.
- Van Ballenberghe, V. 1985. Wolf predation on caribou: the Nelchina case history. *J. Wildl. Manage.* 49:711-720.
- . 1987. Effects of predation on moose numbers: a review of recent North American studies. *Swedish Wildl. Res. Suppl.* 1:431-460.
- . 1989. Wolf predation on the Nelchina caribou herd: a comment. *J. Wildl. Manage.* 53:243-250.
- Van Winkle. 1975. Comparison of several probabilistic home range models. *J. Wildl. Manage.* 39:118-123.
- Weaver, J. L. 1979. Wolf predation upon elk in the Rocky Mountain Parks of North America: a review. Pages 29-33 in M.S. Boyce and L. D. Hayden-Wing, eds. *North American elk: ecology, behavior, and management*. Univ. WY, Laramie. 294 pp.
- Wolff, J. O. 1981. The role of habitat patchiness in the population dynamics of snowshoe hares. *Ecol. Monogr.* 50:111-130.
- Zimmerman, G. M. H. Goetz, and P. W. Mielke. 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. *Ecology* 66:606-611.